

Juvenile infection and male display: testing the bright male hypothesis across individual life histories

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Current tests of the bright male hypothesis focus on assays of adult disease resistance and their relation to male trait development and female choice. We suggest that if parasites have significant harmful effects on juvenile stages of a host, then females selecting males that effectively signal juvenile parasite resistance may gain a significant “good genes” benefit. Currently, there is no information on juvenile and adult infection or resistance in the same male and whether adult male displays signal juvenile parasite resistance. In the present study, we measure infection of the ectoparasitic louse, *Myrsidea ptilonorhynchi*, in individual male satin bowerbirds (*Ptilonorhynchus violaceus*) both as juveniles and nine or more years later as adults. We test hypotheses that examine the role of juvenile parasite infection in mediating sexual selection. We found that (1) juvenile infection is higher than adult infection in the same individuals, (2) adult males able to hold display sites have lower juvenile infection, and (3) juvenile and adult infection in the same individuals are not significantly correlated. In addition, comparisons among a larger set of individuals from a single year show that blood and ectoparasite infections are highly correlated, and both decrease with male age and are inversely related to male courtship success. These results, combined with the evidence that females mate exclusively with bower-holding males support the hypothesis that females use adult male display traits to identify males with a high level of juvenile disease resistance. We suggest that effective tests of the bright male hypothesis should include (1) assessment of infection resistance in both subadult and adult life history stages, (2) tests of whether differences in age-specific resistance are indicated in adult male displays, and (3) tests to determine if females attend to these traits in mate choice. Although these requirements increase the difficulty of testing the bright male hypothesis, they are necessary for a more accurate assessment of the effects of parasites on male display and female choice. *Key words*: bright male hypothesis, mate choice, parasites, sexual selection. [*Behav Ecol* 15:722–728 (2004)]

There is much interest in how parasitic infection might affect the evolution of female choice for male display (see Clayton and Moore, 1997; Hamilton and Poulin, 1997; Milinski, 2001; Thomas et al., 1995). Several hypotheses have been offered, the most prominent being the bright male hypothesis (Hamilton and Zuk, 1982), which proposes that females choose bright males because elaborate displays are effective indicators of heritable male parasite-resistance traits. Hamilton and Zuk (1982) made two predictions that have been used to test the bright male hypothesis. Their interspecific prediction is that brightly plumed species should have fewer parasites than their dull counterparts, and their intraspecific prediction is that males that are most attractive to females should have bright plumage and that these traits are inversely related to parasite infection.

Many studies have attempted, with mixed results, to evaluate the intraspecific prediction of the bright male hypothesis (see Folstad and Kartar, 1992; Hamilton and Poulin, 1997; Møller et al., 1999) and offer differing explanations for why the bright male hypothesis is not better supported. Folstad and Kartar (1992) argue that the immunosuppressive effects of high testosterone levels that contribute to bright displays may cause bright males to have more rather than fewer parasites (but see Braude et al., 1999; Hasselquist et al., 1999; Hilgarth and

Wingfield, 1997; Klein and Nelson, 1998; Saino et al., 2002). Møller et al. (1999, see also Price, 1980) suggest that inconsistent results in tests of the bright male hypothesis may occur because investigators sometimes focus on relatively harmless parasites, but this effect may be mitigated because the numbers of different parasites in individuals are commonly correlated (Hilgarth and Wingfield 1997, Stear et al. 1990). Getty (2002) and Merila and Sheldon (1999) suggest that tradeoffs resulting from the costs of bright display may cause these males to have relatively high infections and could explain deviations from the bright male hypothesis. Also, the bright male hypothesis may be overused in attempts to explain elaborate ornaments, and suggested “failures” of the hypothesis are merely cases in which other sexual selection mechanisms have caused elaborate trait evolution.

Another reason tests of the bright male hypothesis may fail is that they contrast male display quality only with infection in adult males, but such comparisons may not always provide the best test of the bright male hypothesis. If females have evolved to gain the greatest “good genes” benefit from mate selection for parasite resistance, then they should choose male display traits that include information from life-history stages when parasite effects are most harmful. Many species show large age class differences in infection (turkeys: Buchholz, 1995; baboons: Muller-Graf et al., 1997; horses: Proudman et al., 1997; fish: Poulin, 1992) and in many cases there is an age-related reduction in infection (e.g., satin bowerbirds: Borgia and Collis, 1989; red deer: Rehbein et al., 2002; cats: Hecking-Veltman et al., 2001) suggesting that the most severe effects of parasites are often in nonreproductive age classes. The most detailed information on age-specific infection and harm comes from humans and for diseases such as malaria, influenza (*Haemophilus influenzae* type b) diphtheria,

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pertussis, measles, typhoid fever, dysentery, and gastroenteritis (Armstrong et al., 1999; Breman et al., 2001; de Wit et al., 2001; Nelson et al., 2000; Samba, 2001) juveniles suffer more infection than reproductive age classes. The common occurrence of highest infection in young individuals suggests that tests of the bright male hypothesis should consider age-specific patterns of infection, and test for the possibility that adult male display traits indicate resistance to infection not solely in adults but also in juvenile stages. Hamilton and Zuk's (1982: 385) statement that "The ideal disease is one that can be acute and cause heavy juvenile mortality, but persists in chronic form in survivors either as an infection actually latent or as prolonged aftereffects..." suggests that our proposal to consider effects of infection in nonreproductive age classes is consistent with their interpretation of the bright male hypothesis.

Perhaps the most arguable aspect of the proposed modification of tests of the bright male hypothesis is whether adult males can effectively signal differences in resistance from earlier life history stages. Currently, there is no information that directly addresses this issue, but there are several relevant studies. Ohlsson et al. (2002) showed that juvenile condition in male ring-necked pheasants is related to the quality of adult male display. In addition, Nowicki et al.'s (2000) study of complex avian song repertoires suggests that stress in juvenile development affects the quality of adult male display. Although neither of these studies dealt with parasite infection, they are consistent with the suggestion that after-effects of high juvenile infections can be assessed by females observing male display. In humans, there are a variety of diseases that occur primarily in early life-history stages (e.g., acne, small pox, polio) that affect complexion and body symmetry and ultimately adult attractiveness (see Fink et al., 2001).

In the present study, we test the general hypothesis that male display may indicate parasite infection from juvenile life-history stages by using information on infection levels of the parasitic louse (*Myrsidea ptilonorhynchi*) on individual male satin bowerbirds. Male satin bowerbirds are long lived and relatively sedentary, with a long juvenile stage (7 years), and can be readily marked and then recaptured at the same study site over many years. In earlier studies we showed (Borgia and Collis, 1989, 1990) that (1) among males with bowers, females preferred males who had fewer ectoparasitic lice; (2) older age classes of males have fewer ectoparasites than do their younger counterparts; (3) marked males who were not recaptured, and were presumed dead, had a higher mean level of ectoparasite infection than those who returned; and (4) males showed significant year-to-year correlations in parasite infection levels. From these studies we concluded that the female tendency to mate with parasite-free males is consistent with the bright male hypothesis, but could also support the PA hypotheses (Borgia and Collis, 1990). Lower infection in older age classes of males could be explained by higher mortality among less-resistant males, and although we had no direct evidence, it could also result from age-related reductions in infection. Short-term correlations in infection in individuals across years suggested that disease resistance was repeatable (Falconer and MacKay, 1996) and possibly heritable as required by the bright male hypothesis.

First, we determine if there is age-related change in infection in individual males. Although this is consistent with an age-related increase in resistance, it could also occur for other reasons, for example, the death of less-resistant males (see Borgia and Collis, 1990). We compare parasite infection in individual males that were sampled in the 1980s and 1990s to determine if these males show age-related reductions in parasite numbers. Second, we use information on male

plumage changes to identify when in the life history of satin bowerbirds parasite reductions occur. This can indicate if reductions in infection occur at particular ages or show a gradual decrease. Third, a comparison of infection levels within individuals between the 1980s and 1990s is used to determine if numbers of parasites are correlated between life-history stages that are more temporally separated than in our earlier study. If such a correlation exists, then it would allow the possibility that the same traits affect resistance in juveniles and adults and that the same display trait could indicate both juvenile and adult infection levels. Fourth, we test the key hypotheses that male display predicts juvenile and/or adult infection and female choice. We compare males who do and do not have bower sites as adults to determine if differences in infection contributes to male ability to hold these display sites and male courtship success. Fifth, we test for correlations between ectoparasites and blood parasites. Different species of parasites in individuals are often correlated (Hilgarth and Wingfield, 1997; Stear et al., 1990) even though only one might be sufficiently harmful to drive parasite mediated sexual selection.

METHODS

Study site

This study was carried out from September–December in 1983–1986 and 1995–1997 at Wallaby Creek, in the Beaury State Forest, 120 km northwest of Lismore, New South Wales, Australia. Birds were captured in baited traps and removed immediately. The birds were color-banded (if not previously captured), scored for plumage characteristics and numbers of ectoparasites, weighed, measured for wing length, and immediately released. An area 1.5 km in each direction from capture sites was thoroughly surveyed for bowers, and the identity of the owner was determined for each bower. Plumage characteristics and morphological measurements allowed sexing and aging of birds (Vellenga, 1980) and measures of condition. Condition was measured as residuals from the regression of mass on tarsus³ (Patricelli et al., 2004; Uy et al., 2000) Males show age-specific markers, including a change from a black to yellow bill at age five and green to blue (adult male) plumage at age seven. We banded 1694 birds in the 1980s, and of these, 81 were recaptured when we returned in the 1990s. After eliminating females and the males that were not scored for parasites, 36 males remained in our sample.

Parasite scoring

Nits of the louse *Myrsidea ptilonorhynchi* are the only abundant ectoparasite found on satin bowerbirds (Borgia and Collis, 1989, 1990). Initially, the entire bird was inspected for parasites, but ectoparasites were only found regularly around the eye, where these birds have difficulty preening (Borgia and Collis, 1989, 1990). The white lice nits were found on 76% of birds and are easily seen. Counts of these parasites are highly repeatable between captures in the same year (Borgia, 1986). Ticks occurred on about 2% of birds. The hippoboscids flies (*Ornithophilus metallica* and *Ornithomya fuscipennis*) were occasionally found in the plumage on other parts of the bird, but their tendency to fly off the bird made our counts unreliable. These flies regularly carried *M. ptilonorhynchi* attached to their abdomen and are likely vectors for the transfer of lice between birds (Borgia, 1986).

Blood used for counts of blood parasites was obtained by puncturing a wing vein with a small syringe tip. Blood was collected in heparinized capillary tubes as it pooled near the

puncture. A drop of blood was placed on one end of a slide, and the edge of another slide was used to draw out a smear a single cell thick across the slide. These were air dried, fixed, and Giemsa stained. Slides were examined under a $\times 1000$ oil-immersion lens by M.E., who had no prior knowledge of the history of the individual birds. Fields to be viewed on slides were selected along an N-shaped pattern spanning the length of the smear. Fields were selected from areas where there was a single layer of cells until 30 fields had been scored. *Haemoproteus* and *Plasmodium* were the only consistently occurring blood parasites, and we recorded their counts. The slides most suitable for blood parasite analysis were made in 1997, and so, we use information from that year to test hypotheses related to blood parasite infection. Some individuals in the 1997 season had blood taken multiple times, which allowed us to test the short-term repeatability of samples. Counts of *Haemoproteus* from blood samples separated by 2 weeks were highly correlated ($r_s = .70$, $N = 12$, $p = .01$), and there was no change in levels of infection ($Z_w = 0.78$, $N = 13$, $p = .43$) as was found by Gibson (1990) in sage grouse. Slides suitable for blood parasite counts were not available from the 1980s.

Ectoparasite numbers on birds were monitored between 1983 and 1986 and again between 1995 and 1997. Parasite numbers for individual males in each year are the average across samples from that male. Males were captured and had parasites counted on average 1.8 out of the 4 years males were sampled in the 1980s and 1.7 years of the 3 years males were sampled in the 1990s. Because most birds were recaptured multiple times we compared mean infection levels within the 1980s with those within the 1990s for the 36 individual males. Averaging infection levels for comparisons within the 1980s and 1990s is supported by high short-term year-to-year correlation in infection found in earlier studies (Borgia and Collis, 1990).

Male age

The exact age of birds was not known but birds from the 1980s were classed as mature if they had blue plumage and into two groups of juvenile males, 1 to 4 year olds with green plumage and black beaks, and 5 and 6 year olds with green plumage and yellow beaks. All birds that became blue (7 years old) during the span of our 1980s sample were classed as blue plumage birds. This classification allowed us to compare birds of similar age class. The 9-year separation between our 1980s and 1990s samples ensured that even males who might have been 1 year old in 1986 (the last year in the 1980s sample) were at least 10 years old and of an age to hold a bower in the 1990s.

Bower monitoring

Camcorders monitored behavior at 34 bowers of birds from 5 November–22 December 1997. These were controlled by a passive infrared detector coupled with custom-designed electronic circuitry that turned on the modified camcorder when birds approached the bower (see Borgia, 1995). This allowed us to continuously monitor behavior at the bower, including the number of copulations and courtship displays, and the identity of female visitors. Behaviors were quantified by review of video tapes in our laboratory. Courtship success is measured as the proportion of successful copulations resulting from male courtships of females visiting bowers.

Statistics

Statistical comparisons were made by using the Statistica package (Statsoft, 2003). The interclass correlation coefficient

(Lessels and Boag 1987) is used to calculate repeatability that indicates the upper limit for trait heritability (Falconer and Mackay, 1996) to indicate the upper limit for trait heritability. Mann-Whitney U (Z_{mw}) are used to test for differences between samples, and Wilcoxon matched-pairs test (Z_w) provide a non-parametric repeated-measures test. Statistical summary of results over multiple years are provided by Fisher Exact tests (Sokal and Rohlf, 1995: 794). Significance values are reported for two-sided tests unless otherwise noted. Means are reported as mean \pm SE.

RESULTS

Is there an age-related decrease in individual infection?

This long-term analysis of ectoparasites (*M. ptilonorhynchi*) on individual males shows an overall decrease in the parasite load from the 1980s to 1990s. The mean ectoparasite load was higher in our long-term sample among males in the 1980s (26.36 ± 4.3) than when these same males were older in the 1990s (13.63 ± 2.55 ; $Z_w = 2.29$, $N = 36$, $p < .02$) (Figure 1A). When we compared differences in infection levels of all male birds to determine if there was a change in the background level of infection, we found that there was no difference in the overall level of infection among males at Wallaby Creek in the 1980s (17.82 ± 0.71) and 1990s (18.14 ± 0.64 ; $t = -0.331$, $df = 2144$, $p = .74$). Males that ultimately held bowers in the 1990s did not show a reduction in parasites between the 80s and 90s ($Z_w = 0.05$, $N = 16$, $p = 0.96$; $X_{80} = 19.95 \pm 4.72$; $X_{90} = 19.74 \pm 4.61$) (Figure 1B), but those who failed to obtain bowers did ($Z_w = 2.93$, $N = 20$, $p = .003$; $X_{80} = 32.1 \pm 6.82$; $X_{90} = 8.19 \pm 1.68$) (Figure 1C). To control for age effects, we limited our comparison to include only males who were juveniles in 1986. Among these birds, there was no change in infection among those who later held bowers as adults ($Z_w = 0.094$, $N = 14$, $p = .92$) (Figure 2), but there was a significant reduction in parasites among the initially green plumage males who never obtained bowers ($Z_w = 2.85$, $N = 11$, $p = .004$).

In what age classes do parasite reductions occur?

To determine when in individual life histories ectoparasite reductions occurred, we recognized age classes based on beak and plumage coloration and compared 1- to 4-year-old males with 5- to 6-year-old and adult males. Parasite infection in the 1- to 4-year-old juvenile males differed from adults ($Z_{mw} = 3.10$, $N = 28$, $p = .002$) and older juvenile males ($Z_{mw} = 2.73$, $N = 25$, $p = .006$), but infection in older juvenile males was not different from adults ($Z_{mw} = 1.38$, $N = 19$, $p = .16$). Of the decrease in parasites between young juveniles and adults, most (79.8%) occurred between young juvenile (one to four) and older juvenile (five to six) age classes.

Are infection levels correlated between juvenile and adult stages?

Evidence of strong repeatability is consistent with the hypotheses that (1) disease resistance is heritable and (2) the same genes affect disease resistance in juveniles and adults. A correlation of ectoparasite counts for the 1980s and 1990s was used to measure repeatability and was not significant ($r_k = .18$, $N = 36$, $p < .11$). Bower holders showed a similar pattern ($r_k = .29$, $N = 16$, $p < .12$) (Figure 3A), as did males without bowers ($r_k = .17$, $N = 20$, $P < .31$) (Figure 3B). Repeatabilities in infection levels for males between the 1980s and 1990s calculated from the interclass correlation co-

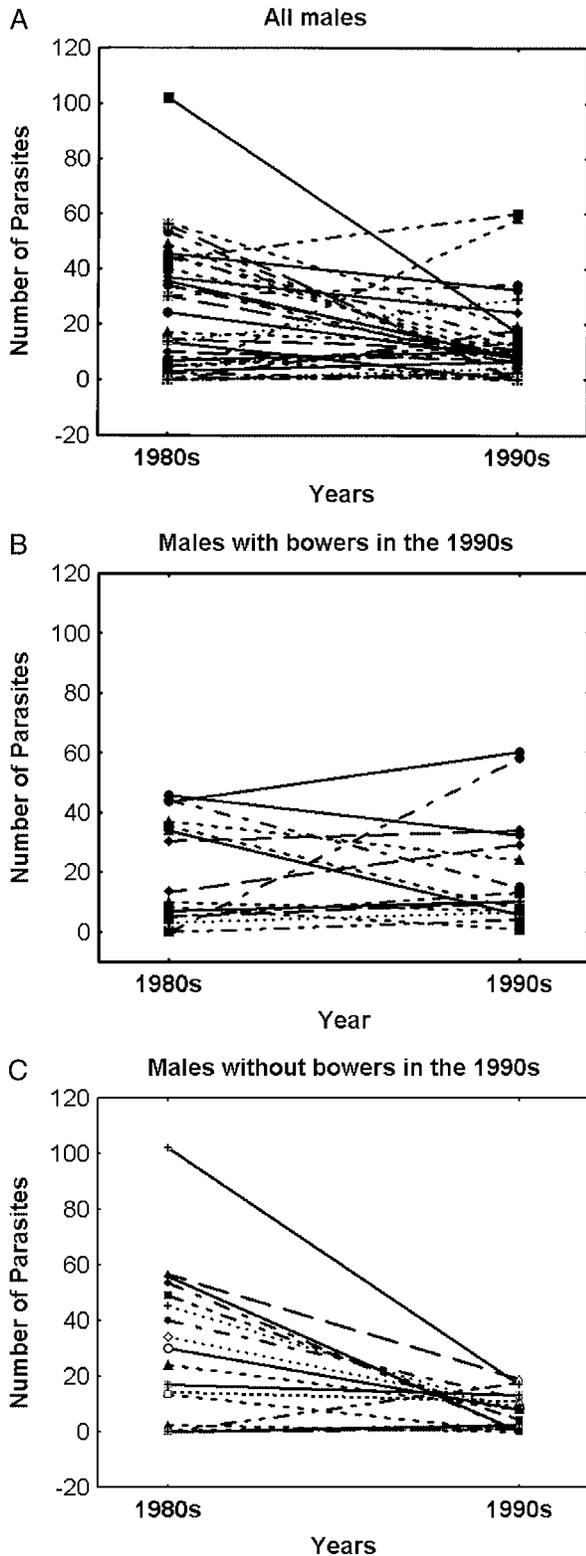


Figure 1
 (A) Age-related reductions in parasites on individual males in the overall sample. Males that became bower holders have initially low infection and maintain that relatively low infection (B), but males who did not become bower holders start with very high infections that lower as they age (C).

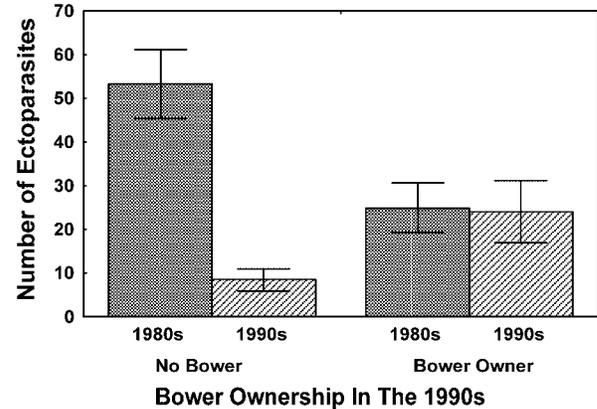


Figure 2
 Comparisons of *M. ptilonorhynchi* infection among males who were juveniles (green plumage) in the 1980s. Males that ultimately come to hold bowers have significantly lower infection as juveniles than males who do not. Males who become bower holders show no difference in infection between juvenile and adult stages, and differ from the nonbower holders who show a dramatic reduction in infection. Infection levels between the two groups of males when they are adults is not statistically different although there is a trend for bower holders to have higher infection than nonbower holders.

efficient were generally low for all males (0.07), males without bowers (0.05), and slightly higher for bower holders (0.32).

Does adult male display indicate juvenile and/or adult infection levels?

We found that males in our sample differed in their tendency to hold bower sites as adults. Display and mating occurs at bower sites so the ownership of sites is key for reproduction (Borgia, 1985, Uy et al., 2000). We compared groups of males that did and did not hold bowers as adults in the 1990s. To control for age effects, we limited our comparison to include only males who were juveniles in 1986. Males who did not obtain bowers in the 1990s had very high infection levels in the 1980s, significantly higher than males that ultimately became bower holders ($Z_{mw} = 2.46$, $N = 25$, $p = .01$) (Figure 1). As blue plumage adults in the 1990s, these two classes of birds did not differ in overall infection, but there was a trend towards higher infection in the group that held bowers ($Z_{mw} = -1.67$, $N = 25$, $p = .09$).

Do blood parasites show infection patterns similar to ectoparasites?

By using a larger sample of 127 males from 1997, we scored for two blood parasites, *Haemoproteus* and *Plasmodium*, and ectoparasites. This information was used to test competing sexual selection hypotheses, including the correlated infection (CI) hypotheses (Borgia and Collis, 1990), which suggests that ectoparasite infection might indicate levels of more harmful blood parasite infection. These blood parasites were observed in 74% and 9% of individuals, respectively, and lice were found on 76%. Infection levels of the two blood parasites were significantly correlated ($r_K = .23$, $N = 101$, $p = .0001$) and counts of *Haemoproteus* were correlated with lice ($r_k = .18$, $N = 101$, $p = .006$) (Figure 4), but counts of *Plasmodium* were not correlated with lice ($r_K = .08$, $N = 101$, $p = .19$). There was an inverse relationship between male age and infection with lice ($r_k = .43$, $N = 101$,

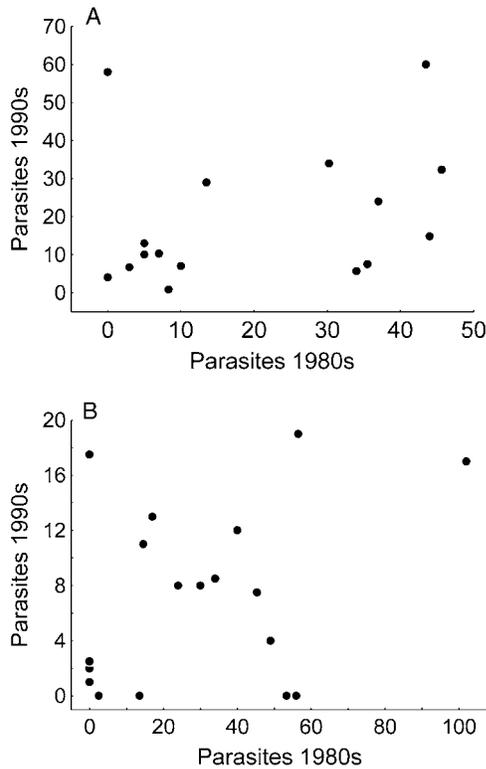


Figure 3
Neither bower holders (A) nor non bower holders (B) showed a significant correlation in infection levels between the 1980s and 1990s.

$p = .0001$), and male age and counts of *Haemoproteus* ($r_k = .21$, $N = 101$, $p = .05$).

Among males monitored by video cameras for courtship success and scored for parasites in 1997, there was a significant negative correlation between male courtship success and lice ($r_K = -.52$, $N = 14$, $p < .01$), similar to the results of our earlier study (Borgia and Collis, 1989). Also, there was a negative correlation between courtship success and the blood parasite, *Haemoproteus* ($r_K = -.53$, $N = 14$, $p < .01$).

Is male condition related to parasite infection?

Over 3 years we compared condition and ectoparasite numbers. In 1995 there was a significant negative relationship ($r_s = -.12$, $N = 270$, $p = .04$); however, in 1996 ($r_s = .04$, $N = 376$, $p = .45$) and 1997 ($r_s = -.08$, $N = 452$, $p = .10$) this relationship was not significant. Combining probabilities across years produced an overall significant negative relationship between condition and infection (Fisher's Exact test: $\chi^2 = -12.6$, $df = 6$, $p = .05$). The small average correlation coefficient across years (0.08) suggests that condition explains little of variation in parasite numbers. We found no relationship between condition and internal parasite numbers.

DISCUSSION

The bright male hypothesis predicts that females can use male display traits to assess parasite resistance. We compared infection levels in individual males as juveniles and later as adults to determine how parasite resistance patterns changed with age and how they are related to male display and mating. Males differed in their ability to hold bower sites as adults.

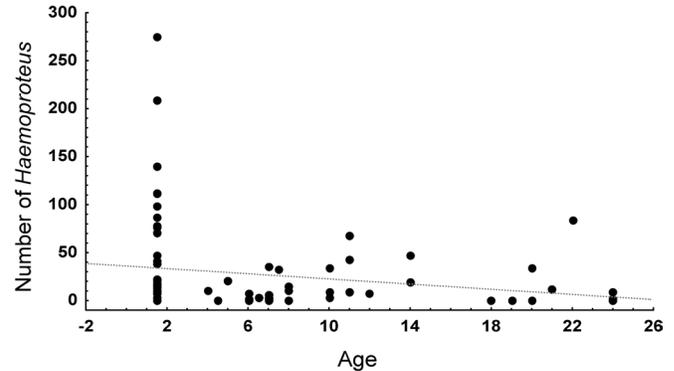


Figure 4
Counts of the blood parasite *Haemoproteus* are correlated with the ectoparasite *Myrsidea* ($r_k = .18$, $N = 101$, $p = .006$).

Males who became bower holders had significantly fewer parasites as juveniles, and there was a nonsignificant trend for these same males to have more parasites as adults. We also found that among bower holding males those with fewer parasites as adults were more attractive to females. Our results are the first to suggest that (1) high infections in juvenile males may reduce their later ability to develop adult display traits, and (2) females may use adult male display to assess juvenile infection.

These results may be important in understanding the mixed pattern of support for the bright male hypothesis. In previous tests of this hypothesis, only information on adult infection is considered, but here we also consider levels of juvenile infection. Our results suggest that the bright male hypothesis might be supported in studies in which it has been rejected using information only on adult infection. Assaying parasite effects over a larger part of individual life histories provides more comprehensive information on their effect on sexual selection. This may be particularly important if the parasite's most harmful effect is during juvenile stages. In addition, comparisons of juvenile infection may allow more reliable assays of disease resistance because this precedes sometimes costly and variable investment in adult male display traits that may trade off against resistance in adults (see Getty, 2002; Merila and Sheldon, 1999; Thompson et al., 1997).

There are multiple hypotheses that could explain a positive relationship between infection and mate choice. The modified bright male hypothesis we suggested here predicts that females should favor males that have low infection as juveniles and adults. The alternative parasite avoidance (PA) hypothesis (Borgia and Collis, 1989), predicts that females choose adult males with low parasite infection, independent of juvenile infection in those males. The PA hypothesis would be unambiguously supported if females choose males with low adult and high juvenile infection, but because we did not find this pattern, we cannot exclude either hypothesis even though the inverse relationship we found between juvenile infection and the ability to develop displays is not predicted by the PA hypothesis.

Because of the trend toward low infection among nonbower holders as adults, it could be argued that females seeking to avoid parasites transferred during mating should mate with these males. But this disregards other proximate advantages derived from mating with bower holders, including (1) protection from forced copulation (Borgia, 1995), and (2) greater ease in relocating males in the series of courtships that lead to mating (Uy et al., 2000, 2001). Protection of the female from the courting male by the bower also allows that

male to closely approach the female, improving her ability to inspect him for ectoparasites (Borgia and Collis, 1989) and allowing females to closely observe intense display (Borgia and Presgraves, 1998; Patricelli et al., 2002). Thus, choosing males at bowers allows improved discrimination that can be important for both PA and bright male choice. Avoidance of nonbower holders could also occur because these males are not inherently more parasite resistant, but have fewer parasites only because they have not assumed the stressful task of holding a bower.

The bright male hypothesis postulates that disease resistance is a heritable genetic trait. Repeatability is commonly used to estimate the upper limit to heritability (Falconer and Mackay, 1996), and in year-to-year comparisons, we found that infection levels in individual male satin bowerbirds were repeatable (Borgia and Collis, 1990). The absence of a significant long-term repeatability could be taken as evidence against the bright male hypothesis. However, the expectation of repeatability of resistance to infection assumes that the same genes are effective in resistance in juveniles and adults. We have no information on the genetics of disease resistance in bowerbirds, but the lowering of infection from juvenile to adult stages among males who do not hold bowers as adults suggests that there may be different age specific genes affecting infection. Thus, a nonsignificant repeatability of infection between juvenile and adult stages does not, by itself, justify rejection of the bright male hypothesis.

The present study follows parasite levels in individuals as juveniles and adults separated by nine or more years and provides a unique view of how infection levels change over lifetimes. Such studies are most likely to be retrospective, and although it is argued that correlational studies may be flawed because inferred causal relationships may be reversed, historical studies address this issue by examining the likelihood of such reversals (Cleland, 2001). For instance, instead of juvenile infection driving male ability to hold bowers, it is possible that male display drives parasite levels, but because juvenile infection occurs years before adult male display, this second pattern of causation is unlikely.

Lowered infection in individuals between the 1980s and 1990s could also occur as a result of coincidental changes in climate or other environmental factors. This is unlikely, however, because (1) in our previous study in the 1980s, we found lower infection levels in older age classes (Borgia and Collis, 1989, 1990); (2) the reduction in parasite numbers we found in this study was not uniform but was restricted to a subgroup of males who were juveniles in the 1980s and who did not hold bowers in the 1990s; and (3) there was no change in population-wide infection between the 1980s and 1990s.

The observed relationships could also be driven by a third variable. Although we were unable to score blood parasites in the 1980s, we found in the present study that lice and *Haemoproteus* were highly correlated in a sample from the 1990s. This suggests that the potentially harmful effects of blood parasites could be driving the observed differences in bower holding ability. We do not know if infections of lice, *Haemoproteus*, or both contribute to the relationship between juvenile infection and adult bower ownership. In this instance, however, if *Haemoproteus* were critical in affecting bower ownership, it would still represent a case in which the juvenile parasite infection was important in affecting adult male display.

The immunocompetence hypothesis (Folstad and Kartar, 1992) suggests that parasite infection is inversely related to testosterone levels. In an earlier study, we showed that juvenile males have lower testosterone levels than do adult males (Collis and Borgia, 1992, 1993) and in the present study,

contrary to the immunocompetence hypothesis, adult males had fewer parasites than juveniles. Unfortunately, we do not have information on testosterone levels for a significant proportion of birds in the present study, so we could not determine if our subgroups of males that had high infection as juveniles and ultimately did not hold bowers as adults differed as juveniles from their like-aged counterparts in testosterone levels. Our earlier study (Collis and Borgia, 1993) showed that adult males without bowers had lower testosterone levels than males who held bowers. This suggests the possibility that high juvenile infections might ultimately lower adult male testosterone levels, causing males with high early infections to be less competitive in the establishment of bower sites.

In conclusion, several reviews have given mixed support to the bright male hypothesis. Here we suggest that the lack of clear support for the bright male hypothesis may, in part, be owing to the exclusive use of adult infection or resistance as a measure of parasite resistance. We propose that more effective tests of the bright male hypothesis include information on parasite infection from across individual life histories including juvenile stages. Our results showing that juvenile infection is a better predictor of bower ownership than is adult infection supports this claim. We encourage more long-term studies that sample infection across individual life histories because we believe that these will provide more realistic tests of the bright male hypothesis and test the generality of our conclusions. We also recognize limitations to this approach because of the difficulty and cost of repeated relocation and recapture of individuals over their lifetimes (particularly for long lived organisms), and because tests of immunity such as response to artificial antigens (see Hasselquist et al., 1999) become complicated when individuals are tested multiple times. Even so, assessment of infection/resistance across individual life histories fits with the growing recognition that sexually selected traits may be shaped over individuals' entire life histories (Badyaev and Qvarnström, 2002; Kokko, 1998; Ohlsson et al., 2002), and therefore tests of sexual selection models need to take this into account.

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